Crop Damage Estimates for Crown Rot of Wheat and Barley in the Pacific Northwest

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ABSTRACT

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Crown rot of wheat and barley in the Pacific Northwest is caused by a complex of *Fusarium pseudograminearum*, *F. culmorum*, *F. avenaceum*, *Bipolaris sorokiniana*, and *Microdochium nivale*. Yield-loss estimates were made by evaluating yield components on tillers collected from commercial fields and sorted by disease severity classes, and by comparing yields for field plots inoculated with *F. pseudograminearum* with yields in naturally infested soil. Increasing crown rot severity caused an increase in grain protein content and reduction in grain yield, kernels per head, kernel weight, test weight, tiller height, and straw weight. Crown rot reduced winter wheat yield as much as 1,550 kg/ha (35%, \$219/ha) in commercial fields, with a 13-field mean of 9.5% (\$51/ha). Inoculation reduced yields as much as 2,630 kg/ha (61%, \$372/ha) over that caused by the native pathogen flora. Rain-induced crusting of the soil surface greatly amplified pre-emergence damping-off caused by *F. pseudograminearum*. Crown rot caused the greatest losses during seasons of lowest precipitation but also damaged crops under wet conditions. Above-ground symptoms were not always apparent under conditions of moderate infection and yield constraint. Damage from crown rot in the Pacific Northwest is more widespread and damaging than previously recognized.

Additional keywords: common root rot, dryland foot rot, Fusarium crown rot, *Hordeum vulgare*, *Triticum aestivum*

A complex of crown- and root-infecting fungi causes chronic and occasionally severe damage to wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) in the Pacific Northwest (PNW) states of Idaho, Oregon, and Washington (9–11). Primary pathogens in the complex (11,31) include *Fusarium pseudograminearum* (O'Donnell & Aoki) (= *F. graminearum* group I, = *Gibberella coronicola*), *F. culmorum* (Wm. G. Sm.) Sacc., and *Bipolaris sorokiniana* (Sacc.) Shoemaker (= *Cochliobolus sativus*). Pathogens of less importance include *F. avenaceum* (Fr.:Fr.) Sacc. (= *Gibberella avenacea*) and *Microdochium nivale* (Fr.) Samuels & I. C. Hallett (= *Monographella nivalis*). These pathogens may occur singly, but they often co-exist in the same fields and even within individual plants, and the dominant pathogens at a specific

location can vary from year to year (31). Regionally, *F. pseudograminearum* is more widespread than *F. culmorum*, which is more prevalent than *B. sorokiniana*. Each of the pathogens is capable of infecting leaves and inflorescences, but low mean-annual precipitation (250 to 500 mm) and winter-dominant rainfall distribution in the PNW wheat belt usually restrict infections to the root cortex, scutellum, subcrown internode, crown, or lower culm (R. W. Smiley, *personal observation*). Crown rot is the generally accepted name when *Fusarium* spp. are dominant members of the complex and common root rot describes the complex when *B. sorokiniana* is dominant. Other regional names used in the PNW wheat belt include dryland foot rot, dryland root rot, foot rot, Fusarium crown rot, and Fusarium root rot.

Crown rot occurs in most cereal-producing regions of the world, including Australia (1,7,36), Europe (8,26), North America (11,31), South Africa (17,20,34), West Asia, and North Africa (21,23). Despite crown rot being pandemic, documentation of associated economic damage is very limited.

Cook (9) reported yield comparisons in the PNW for two sets of adjacent winter wheat fields differing in populations of *F. culmorum*. Yields were 17 and 50% (400 and 2,023 kg/ha) less in fields with high

pathogen populations compared with yields in adjacent fields with low or undetectable populations.

We are not aware of any published reports for yield loss estimates in PNW fields infested primarily by *F. pseudograminearum*. Kane et al. (16) reported yield reductions up to 24% (790 kg/ha) from crown rot in winter wheat plots planted with seed infested by *F. graminearum* in northwestern New York. Rainfall in upstate New York (935 mm mean annual precipitation) is much higher than in the PNW (250 to 500 mm). Moreover, precipitation in New York has a summer-dominant distribution with no summer months averaging less than 55 mm, compared with the winter-dominant distribution in the PNW, where precipitation during summer months averages less than 15 mm. Burgess et al. (7) reported that *F. pseudograminearum* crown rot caused up to 26% yield reduction in individual wheat fields in subtropical southern Queensland, Australia, where wheat is grown during the lowest-rainfall winter months when precipitation averages more than 25 mm/month in areas with 450 to 650 mm of annual precipitation (2). Burgess et al. (7) estimated that, during years of especially heavy disease occurrence, wheat production for the entire state was reduced by about 5%. Dodman and Wildermuth (12) used an individual tiller method to estimate yield reductions of up to 46% in southern Queensland. Klein et al. (18) also used the individual tiller method to determine that crown rot reduced potential yield from 0 to 89% at nine northern New South Wales sites surveyed over 4 years, with an overall average yield reduction of 19% for 28 site-years.

Burgess et al. (5) concluded that there “is very little objective information on the economic importance of crown rot on a regional basis, and thus it is not possible to accurately estimate the losses caused by the disease.” Experimental damage estimates are particularly lacking for *F. pseudograminearum* in winter-dominant precipitation regions such as the PNW. Damage estimates for the PNW could provide several important types of information. Effects on grain yield, test weight, and kernel weight could provide information on profitability of individual farms and the agricultural industry. Effects of crown rot on grain protein content could

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predict flour performance characteristics during milling and baking. Straw yield reduction could affect grower compliance with provisions of Federal programs for improving air quality and soil and water conservation. Investment in disease management research demands quantitative documentation of economic damage caused by crown rot.

The objective of this research was to estimate yield losses from crown rot in winter and spring wheat and winter barley in Oregon and Washington. Estimates from commercial fields were based on measurement of yield components on individual tillers that differed in crown rot severity. Estimates also were made by inoculating naturally infested field plots and comparing yield differentials between inoculated and noninoculated plots.

MATERIALS AND METHODS

Commercial fields. Crown rot damage was assessed on commercial fields in Oregon and Washington using an individual tiller procedure (12). This procedure involved determining potential yield by multiplying the yield per healthy tiller by the total number of healthy and diseased tillers. Percentage of yield loss then was calculated by dividing the difference between potential and actual yield by the potential yield, and multiplying the result by 100. Multiple samples were collected from 13, 10, and 3 fields during 1994, 1995, and 1996, respectively.

1994—Winter wheat. Thirteen fields of mature winter wheat were arbitrarily selected for sampling. All fields were managed as a 2-year rotation of winter wheat and cultivated summer fallow. Field selections represented a wide geographic area but no prior knowledge of disease history, current disease incidence or severity, or wheat cultivar. Seven fields were in Gilliam and Sherman Counties of Oregon, and six were in Benton and Walla Walla Counties of Washington. Information regarding wheat production, climates, and soils in these counties is presented elsewhere (30,31). Cultivars were identified after sampling. The 13-field sample included the following cultivars and number of fields in the indicated county and state: 'Gene' (1 field, Benton County, WA), 'Lewjain' (1 field, Benton County), 'Madsen' (2 fields, Sherman County, OR; 1 field, Walla Walla County, WA), 'Malcolm' (1 field, Gilliam County, OR), 'Stephens' (3 fields, Gilliam County; 1 field, Sherman County; 1 field, Walla Walla County), and 'Weston' (2 fields, Benton County).

All plants with intact roots (to 10 cm of depth) in a 3-m row section were collected from two arbitrarily selected areas in each of 13 fields (26 samples). Mature plants in each 3-m row section were referred to as "bundle samples" to represent the manner in which they were stored prior to analysis.

Numbers of plants with and without culm-browning symptoms of crown rot were recorded for each bundle sample. The 13,384 tillers in these 26 samples then were separated and leaf sheaths removed to expose culms. Tillers were separated into five groups representing crown rot classes based on extent of culm-browning. Disease severity classes were D_0 = none; D_1 , D_2 , and D_3 = browning up to the first, second, or third node, respectively; and D_4 = browning up to the fourth node or above. Measurements of plant characteristics within each group included numbers of tillers, percentage of tillers with heads, straw weight, tiller height, grain weight, grain protein (calculated by multiplying percent N in grain by 5.7), and kernel weight.

Representative numbers (approximately 10 per field) of subcrown internode lesions and core tissues from rotted crowns were plated onto peptone pentachloronitrobenzene agar medium to isolate *Fusarium* spp. and *M. nivale* (22), and Czapek-Dox (amended with benomyl) agar medium to isolate *B. sorokiniana* (32). Identities of *Fusarium* spp. and *M. nivale* isolated from plated tissues were determined using standard morphological characteristics on wheat-leaf agar (22).

Estimates of crop damage caused by crown rot were based on the simplified form (12,18) of the "multiple-predictor model" (33) used to estimate crown rot damage in Australia. We first assessed the number of headed tillers (T_{Dx}) and grain weight/tiller (G_{Dx}) for each of five disease severity classes, D_0 to D_4 . Measured yield (MY) for each bundle was calculated by adding grain weights obtained from all heads in each severity class: $MY = G_{D0} + G_{D1} + G_{D2} + G_{D3} + G_{D4}$. Potential yield (PY) was calculated by multiplying total headed tillers by the grain weight/tiller for healthy tillers (G_{D0}): $PY = (T_{D0} + T_{D1} + T_{D2} + T_{D3} + T_{D4})G_{D0}$. Percentage yield loss (YL) from crown rot then was calculated as $YL = [(PY - MY)/100]/PY$.

YL estimates were converted into economic damage estimates by multiplying calculated yield reductions (kg/ha) by the prevailing market price for wheat. No adjustment was attempted where wheat quality (test weight or grain protein content) also was affected by crown rot.

Plant growth and yield characteristics for each disease severity class were analyzed by analysis of variance for the randomized complete block model, using CoStat Statistical Software (version 6.101; CoHort Software, Monterey, CA). The 26 samples were considered replicates for the analysis. When treatment effects were significant at $P < 0.05$, means were separated using the Fisher's least significant difference (LSD) test. Variables were also evaluated by regression analysis using the linear model.

1995—Winter wheat. A portion of the 1994 survey was repeated. Ten fields of

Stephens winter wheat were identified in February when seedlings were nearly dormant in frozen soil. The fields were in Gilliam and Sherman Counties, OR and Walla Walla County, WA. Fields were selected on the basis of cultivar planted and a planting date between 1 and 15 September 1994. None of the fields were on farms sampled during 1994. Seedling samples were collected from two 15-m circular sampling zones in each of the 10 fields during March 1995, for a total of 20 samples. All plants with intact roots were collected from 10 20-cm row segments in each of the 20 sampling zones; about 120 plants for each zone, or 240 plants per field. Composites from each of the 20 sampling zones were evaluated individually. Flags were installed to mark a 3-m row segment in each zone for use in subsequent sampling.

Plants were washed and 100 plants per sample were evaluated for plant height, numbers of tillers, and crown rot symptoms, including dark lesions on subcrown internodes. Each crown was dissected to determine the incidence of plants for which the internal crown tissue was rotted. Identities of fungal pathogens were determined as described earlier. When mature, all plants were dug from the 3-m row section in each of the 20 sampling zones. The 10,961 tillers in the 20 bundle samples were evaluated and analyzed as described for the 1994 survey.

1995—Spring wheat. Sampling procedures used for winter wheat during 1995 were repeated for a single field of hard red spring wheat (cv. Westbred 936R) in western Umatilla County, OR. Data were collected during spring and summer as described for experiments with winter wheat. Bundle samples of mature plants were collected from three 3-m-long row sections, providing 883 tillers for evaluation.

1996—Winter wheat. Survey procedures used for winter wheat during 1995 were repeated. Two bundle samples were collected from each of three fields of Stephens winter wheat (six samples, with 3,047 tillers). Two fields were in western Umatilla County, OR and one field was in Benton County, WA.

Inoculated field trials. *Inoculum source and characterization.* Nonquantified native populations of the pathogens in soil were supplemented with inoculum of *F. pseudograminearum* to ensure adequate crown rot incidence and severity in field trials and to reduce heterogeneity of pathogen distribution typical of native populations.

F. pseudograminearum was isolated from infected crowns of winter wheat during a survey of pathogens associated with crown rot in Oregon and Washington during 1993 and 1994 (31). Isolates initially were identified from morphological features on 0.5-strength potato-dextrose and wheat-leaf agar media (22). Identities were confirmed using polymerase chain reaction

procedures (27,37). All isolates were stored on silica beads at 4°C and autoclaved barley seed at -80°C. Five isolates (93-82-03, 94-006-13, 94-32-06, 94-44-09, and 94-81-11) were selected as inoculum sources to achieve a range in both geographic origin and virulence ratings to wheat seedlings in greenhouse tests (*unpublished data*). Isolates were from different farms in Sherman and Wasco Counties in Oregon (three isolates) and Walla Walla County in Washington (two isolates). In greenhouse tests, the isolates had virulence ratings of 4.8 to 6.0 on a 0-to-7 scale, where 0 = no damage to seedlings and 7 = strong crown rot symptom development and stunting of seedling growth.

Each isolate was grown on 0.2-strength potato-dextrose agar medium and seeded individually onto twice-autoclaved millet seed. Colonized millet was air dried and stored at room temperature (approximately 24°C) in paper bags. Isolates were sieved to eliminate clumps and then blended in equal proportions to form a single composite before being applied to soil.

Inoculation rate. An appropriate application rate was estimated using dose-response experiments with winter wheat cv. Stephens at three locations during 1995 to 1996. Experiments were performed at a commercial farm near Echo, OR, and the Oregon State University Columbia Basin Agricultural Research Center (CBARC) stations near Moro and Pendleton. All soils were Walla Walla silt loam (coarse-silty, mixed, superactive, mesic Typic Haploxerolls). Mean annual rainfall is 255 mm at the farm near Echo, 282 mm at CBARC-Moro, and 442 mm at CBARC-Pendleton.

The inoculation procedure has been described (12,35). Inoculum was placed above the wheat seed so the coleoptile would pass through the zone of inoculation prior to seedling emergence. Wheat seed was treated with benomyl (Benlate; DuPont Crop Protection, Wilmington, DE) fungicide at 0.225 g a.i./kg of seed to reduce or eliminate seedling damping-off associated with crown rot pathogens. Wheat was planted at 250 seeds/m² and a depth of 5 to 7 cm using a John Deere HZ deep-furrow drill equipped with a cone-seeder and four openers at 36-cm-row spacing. Inoculum then was applied by hand in each drill furrow. Inoculum rates were 0, 0.2, 0.3, 1, 1.7, 3.3, 8, 17, and 33 g/m of row. Each gram of inoculum contained about 200 millet seed. The control treatment consisted of sterilized millet seed not colonized by the pathogen. Control soils were naturally infested with *F. pseudograminearum*, which was not quantified because the pathogen survives as mycelium in pieces of crop refuse (5,10) and is not easily quantified. The millet-seed carrier for all treatments was placed about 3 cm above each row of wheat seed and was buried shallowly by raking soil laterally from between drill rows. All

treatments were replicated three times in 1.5-by-6-m plots.

Data during the autumn included seedling emergence and plant stand at two 1-m-row segments marked immediately after planting. During the spring (March), 10 plants were collected from each of three locations in each plot to determine numbers of tillers/plant, incidence of rotted crowns, and incidence and severity of crown rot symptoms on subcrown internodes. Bundle samples collected during July from two 1-m marked segments in each plot were used to measure head height, straw weight, grain weight/head, and kernel weight. Data were analyzed as described previously.

Cultivar nurseries. From 1999 to 2004, winter and spring wheat and winter barley cultivars and advanced breeding lines were examined for responses to crown rot caused primarily by *F. pseudograminearum*. Wheat entries from Oregon State University and Washington State University breeding programs were planted into conventionally tilled (chisel plow and rod weeder) summer fallow following winter wheat harvested 14 months earlier at CBARC-Moro and CBARC-Pendleton. Procedures were as described for the inoculation-rate experiment, except the inoculum was dispensed mechanically. For this article, responses of all cultivars in selected experiments were averaged to provide comparisons of control (noninoculated) treatments with the influence of *F. pseudograminearum* inoculation on plant growth, disease incidence and severity, and grain yield and test weight.

Multiple wheat, triticale, or barley entries were planted with and without the millet-seed inoculum. The experimental design was a split-plot with each grain entry as the main plot and inoculum treatments as subplots in blocks replicated four times. Plots were 1.5 by 6 m (four rows/treatment) during 2001 and 0.8 by 6 m (two rows/treatment) during subsequent years. Millet seed inoculum was metered from a Gandy fertilizer dispenser mounted on the grain drill, and dispensed through an adjustable-depth tube mounted behind each drill opener. For the inoculum treatment, colonized millet seed was dispensed at 2.3 g/m of row and banded 2 cm above the wheat seed. Inoculum was dispensed into all four drill rows for four-row inoculated plots and into two adjacent rows on the same side of the drill for two-row plots. Control treatments in each plot type were planted without dispensing millet seed.

Seventeen winter wheat and one triticale cultivar or breeding line were planted on 24 September at a depth of 8 cm and seed-zone temperature of 15°C at CBARC-Pendleton during 1999, 22 September at a 4-cm depth and 16°C seed-zone temperature at CBARC-Pendleton during 2000, 18 September at an 8-cm depth and 23°C seed-zone temperature at CBARC-

Pendleton during 2001, and 1 October at a 4-cm depth and 15°C seed-zone temperature at CBARC-Moro during 2001. During 2003, winter barley (eight entries) was planted at CBARC-Pendleton on September 15 at a 4-cm depth and 19°C seed-zone temperature. During 2004, spring wheat (four entries) was planted on March 23 at a 3-cm depth and 12°C seed-zone temperature at CBARC-Pendleton and a 3-cm depth and 9°C seed-zone temperature at CBARC-Moro. Standard fertilizer and weed control practices were utilized for each experiment.

Plant emergence was assessed by non-destructive measurements 14 to 30 days following planting. Fifteen plants per plot were collected and assessed for growth and disease characteristics during the spring, as described previously. In addition, as plants matured, percentages of whiteheads were estimated by counting whiteheads and total heads in one row for each plot. Plots were harvested in August using a Hege 140 plot combine. Grain yields, test weights and kernel weights were measured using standard procedures.

Data were analyzed with an analysis of variance, using a split-plot design for the Co-Stat Statistical Software (version 6.101; CoHort Software). When treatment effects were significant at $P < 0.05$, means for treatments were separated using the Fisher's LSD test.

RESULTS

Commercial fields. 1994—*Winter wheat.* The crop received much lower than normal amounts of rainfall during most months of the crop year. Overall precipitation for the selected sites was 29 to 51% less than for the long-term averages at the experimental locations. For instance, for the winter wheat crop year, 1 September to 31 August, sites near Moro (Sherman County) and Pendleton (Umatilla County) received 150 and 318 mm, respectively.

Percentages of plants with crown rot ranged from 24 to 98%, with a 13-field mean of 76%. Disease incidence was least in fields of Gene (24%) and greatest in fields of Malcol (98%). Large site-specific differences occurred for Madsen (range of 37 to 98% infected plants for three fields) and Stephens (62 to 96% for five fields). Similar ranges occurred for percentages of symptomatic tillers: 12 to 79% for Madsen and 39 to 81% for Stephens.

Increasing severity of crown rot was associated with a reduction in all plant growth and yield characteristics examined (Table 1) when data from 13,384 tillers from 26 samples in 13 fields were composited. This included numbers of kernels/head, kernel weight, grain weight/head, percentage tillers with heads, straw weight/tiller, and tiller height. Calculated reduction in grain yield became greater as disease severity increased. Overall yield

reduction due to crown rot in the 13 arbitrarily selected fields ranged from 0 to 35%, with an average of 9.5%. Percentage reduction in grain yield was highly correlated with percentages of tillers in disease severity class D₄; %YL = 3.48 + 1.08 (%D₄), $R^2 = 0.66$, $P < 0.001$, 25 df.

Grain protein content (Table 1) increased with increasing disease severity class ($P = 0.08$). Average protein content for bulk samples from the 13 fields ranged from 8.2 to 16.7%. Six fields had protein contents of 12% or lower, and four exceeded 14%. Protein content was not associated with cultivar, wheat market class, or location.

Analyses also were performed for five subgroups selected from the 13 surveyed fields. Subgroup one was composed of 4,690 tillers from the five fields planted to

Stephens. Subgroup two was composed of 6,151 tillers from six fields with high protein, including two fields each of Madsen (13.8 and 15.6% protein), Stephens (13.2 and 16.7%), and Weston (14.6 and 16.2%). Subgroup three was composed of 4,934 tillers from five fields with low protein, including single fields of Lewjain (11.5% protein) and Malcolm (11.9%) and three fields of Stephens (8.2, 10.6, and 11.7%). Subgroups four and five were composed of four fields each that had either "low" or "high" crown rot severity in Sherman and Gilliam Counties. The low-severity subgroup (2 to 3% yield loss) included 4,124 tillers from two fields of Madsen and two fields of Stephens. The high-severity subgroup (13 to 35% yield loss) included 3,607 tillers from two fields of Stephens and one each for Madsen and Malcolm.

Relationships between disease severity classes and plant growth and yield variables were similar for within the 13-field multicultivar composite (Table 1), the 5-field multi-location Stephens subgroup (*data not shown*), and the 5-field low-protein and 6-field high-protein subgroups (Table 2). In each subgroup, the protein content was significantly ($P < 0.05$) higher for tillers in disease severity classes D₃ and D₄ than for tillers in classes D₀ to D₂. Grain yields were highly correlated with percentages of tillers in disease severity class D₄ only for subgroups from the Stephens (Fig. 1) and low-protein sites ($R^2 = 0.66$, *data not shown*).

Percentages of plants with crown rot differed significantly at $P = 0.07$ in the four-field subgroups composed of fields with low and high crown rot severity; 63 versus

Table 1. Crown rot severity and yield components for 13,384 winter wheat tillers from two 3-m row segments in each of 13 arbitrarily selected fields in Oregon and Washington during 1994

Plant characteristic	Disease severity class for tillers ^x					LSD _{0.05}
	D ₀	D ₁	D ₂	D ₃	D ₄	
Tillers in class (%)	47 a	25 b	17 b	6 c	5 c	8.1
Kernels/head	21.0 a	20.3 a	20.1 a	16.4 b	6.6 c	2.6
Grain protein (%) ^y	12.6 a	12.5 a	13.0 a	13.3 a	14.2 a	ns
Kernel weight (mg)	43a	42 a	41 a	36 b	33 c	2.9
Grain weight (mg/head)	899 a	806 a	794 a	673 b	399 c	119
Tillers with heads (%)	96 a	82 b	85 b	80 b	84 b	8.1
Straw weight (g/tiller)	1.7 a	1.6 a	1.7 a	1.6 a	0.9 b	0.3
Tiller height (cm)	73 a	72 a	71 a	68 b	64 c	2.5
Reduction in grain yield from disease (%) ^z	0 a	10 ab	12 b	28 c	30 c	10.1

^x Crown rot severity classes were D₀ = none; D₁, D₂, and D₃ = browning up to the first, second, or third node, respectively; and D₄ = browning up to the fourth node or above. Means followed by the same letter within a row are not significantly different at $P=0.05$ according to Fisher's least significant difference (LSD); ns = not significant.

^y Grain protein content differed significantly at $P = 0.08$, with LSD_{0.10} = 0.7.

^z Relative comparison of yields for groups of individual tillers exhibiting (D₁ to D₄) or not exhibiting (D₀) visual symptoms of crown rot.

Table 2. Crown rot severity and yield components for 11,085 winter wheat tillers in two subgroups of 13 arbitrarily selected fields in Oregon and Washington during 1994^x

Plant characteristic	Disease severity class for tillers ^y					LSD _{0.05}
	D ₀	D ₁	D ₂	D ₃	D ₄	
Low-protein fields						
Tillers in class (%)	38 a	26 b	23 b	6 c	7 c	7.9
Kernels/head	19.7 a	18.5 a	19.1 a	16.5 a	8.8 b	4.7
Grain protein (%)	10.8 a	10.5 a	11.0 a	11.6 b	12.9 c	0.7
Kernel weight (mg)	45 a	44 ab	43 ab	37 b	24 c	6.9
Grain weight (mg/head)	871 a	784 ab	795 ab	605 b	288 c	194
Tillers with heads (%)	98 a	88 b	89 b	88 b	93 ab	7.7
Straw weight (g/tiller)	1.8 a	1.7 a	1.7 a	1.7 a	1.2 b	0.4
Tiller height (cm)	72 a	72 a	71 a	55 b	40 b	15.4
Reduction in grain yield from disease (%) ^z	0 a	14 ab	14 ab	30 bc	39 c	19.0
High-protein fields						
Tillers in class (%)	38 a	31 a	18 b	8 c	5 c	9.3
Kernels/head	22.4 a	21.4 a	21.1 a	17.5 b	14.8 b	3.4
Grain protein (%)	13.4 a	13.5 ab	13.7 abc	13.8 bc	13.9 bc	0.4
Kernel weight (mg)	42 a	40 a	41 a	38 a	15 b	7.3
Grain weight (mg/head)	932 a	851 a	858 a	665 b	226 c	178
Tillers with heads (%)	99 a	95 a	96 a	98 a	99 a	ns
Straw weight (g/tiller)	1.8 a	1.6 a	1.2 b	1.0 bc	0.8 c	0.3
Tiller height (cm)	76 a	75 a	73 a	70 a	36 b	17.2
Reduction in grain yield from disease (%) ^z	0 a	9 a	11 a	27 b	34 b	16.3

^x Subgroups were composed of 4,934 tillers from five fields with low protein content (<12%), and 6,151 tillers from six fields with high protein content (>12%).

^y Crown rot severity classes were D₀ = none; D₁, D₂, and D₃ = browning up to the first, second, or third node, respectively; and D₄ = browning up to the fourth node or above. Means followed by the same letter within a row are not significantly different at $P = 0.05$ according to Fisher's least significant difference (LSD); ns = not significant.

^z Relative comparison of yields for groups of individual tillers exhibiting (D₁ to D₄) or not exhibiting (D₀) visual symptoms of crown rot.

87%, respectively; $LSD_{0.10} = 21$. A shift in disease severity classes also occurred among tillers in these subgroups. Compared with high-severity fields, low-severity fields had significantly higher percentages of D_0 (67 versus 36%) and D_1 (29 versus 15%) tillers and fewer D_3 (3 versus 12%) and D_4 (2 versus 36%) tillers. Overall yield losses for the low- and high-severity subgroups were calculated at 3 and 21%, respectively ($LSD_{0.05} = 10$), for a difference of 777 kg/ha.

During 1994, average market price was \$0.1413/kg (\$3.85/bushel) for soft white wheat and \$0.1643/kg (\$4.50/bushel) for hard red wheat. Economic damage for the 13 arbitrarily selected fields during 1994 ranged from \$3 to \$219/ha, with an average of \$51/ha. The difference in yield loss between four heavily affected and four

lightly affected fields was valued at \$110/ha.

Dominant pathogens in rotted crowns and subcrown internodes (Table 3) were *F. pseudograminearum* (9 of 13 sites), *F. culmorum* (1 site), *M. nivale* (1 site), and mixtures of either *F. pseudograminearum* and *F. culmorum* (1 site) or of *B. sorokiniana* and *F. avenaceum* (1 site). Highest crop damage estimates (20 and 35%, or \$114 and \$219/ha) occurred in the two fields where *F. culmorum* was among the dominant pathogens isolated from symptomatic tissues. The highest damage estimates for fields infested primarily by *F. pseudograminearum* or *B. sorokiniana* were 13 and 16% (\$48 and \$58/ha), respectively.

1995—Winter wheat. Ten fields planted to Stephens were surveyed during 1995.

Crops in the selected fields received 18 to 39% greater precipitation than the long-term averages for each locality. There was no abnormally dry interval during the crop year. Most of the 10,961 tillers from the 20 samples were in the lowest crown rot severity classes; $D_0 = 69\%$, $D_1 = 19\%$, $D_2 = 9\%$, $D_3 = 1\%$, and $D_4 = 2\%$ (data not shown). Although trends were similar to those for the Stephens subgroup during 1994, increasing disease severity classes were associated with a statistically significant ($P < 0.05$) reduction only for kernel weight, tiller height, and straw yield (data not shown). Grain protein content became significantly greater with increasing disease severity. Calculated reductions in yield associated with each disease severity class all were less than 3%, and overall yield loss from crown rot for the 20 samples ranged from 0 to 10% (482 kg/ha), with a mean of 2% (49 kg/ha). Fields infested by either *F. culmorum* or *F. pseudograminearum* were each among those with lowest and highest crop damage estimates.

Using the same market price as for 1994, economic damage estimates for the 20 samples of Stephens soft white winter wheat collected during 1995 ranged from \$0 to \$68/ha, with an average of \$7/ha.

1995—Spring wheat. Three samples from a single field of hard red spring wheat were evaluated during 1995. *F. pseudograminearum* was the only crown rot pathogen detected. Half of the 883 tillers exhibited lower-stem browning symptoms associated with crown rot (Table 4). Nearly all tillers produced heads, and values for most grain yield variables became significantly lower as disease severity class increased. Grain protein content and calculated yield loss from crown rot increased with increasing disease severity. Straw weight and plant height did not differ among disease severity classes.

Fig. 1. Relationship between percentages of tillers in disease severity class D_4 and calculated yield loss due to crown rot for 10 samples from five 'Stephens' winter wheat fields in Oregon and Washington during 1994.

Table 3. Economic damage estimates for 13 commercial winter wheat fields in eastern Oregon and Washington during 1994

Cultivar	Market class	Dominant pathogen ^y	Yield (kg/ha) ^x		Loss from crown rot		
			Measured	Potential	Weight (kg/ha)	Percent	Value (\$/ha) ^z
Gene	Soft white	Fp	4,560	4,585	25	0.5	3.54
Lewjain	Soft white	Fp	3,911	4,316	405	9.4	57.27
Madsen	Soft white	Fc	3,169	3,978	809	20.3	114.39
Madsen	Soft white	Fp	3,844	3,911	67	1.7	9.47
Madsen	Soft white	Fp	3,024	3,102	78	2.5	11.03
Malcolm	Soft white	Fp	2,293	2,630	337	12.8	47.65
Stephens	Soft white	Fc/Fp	2,832	4,383	1,551	35.4	219.31
Stephens	Soft white	Fp	2,325	2,360	135	1.5	19.09
Stephens	Soft white	Bs/Fa	2,220	2,630	410	15.6	57.97
Stephens	Soft white	Mn	3,324	3,506	182	5.2	25.73
Stephens	Soft white	Fp	2,495	2,573	78	3.0	11.03
Weston	Hard red	Fp	4,316	4,518	202	4.5	33.19
Weston	Hard red	Fp	2,629	2,967	338	11.4	55.53
13-field mean	...	...	3,149	3,497	348	9.5	51.17

^x Yields for each of 13 fields represent means of two samples each consisting of all plants collected from a 3-m row segment. Measured yield was calculated from grain harvested and area of land represented by the row segment. Potential yield was calculated based on yields of healthy tillers multiplied by numbers of healthy plus crown rot-affected tillers.

^y Principal pathogenic fungi isolated from crown rot-affected tissues at each site were *Bipolaris sorokiniana* (Bs), *Fusarium avenaceum* (Fa), *F. culmorum* (Fc), *F. pseudograminearum* (Fp), and *Microdochium nivale* (Mn). Species were co-dominant where two species are indicated.

^z Economic loss was calculated using a uniform grain test weight of 775 kg/m³ (60 pounds/bushel) and grain price of \$0.1413/kg (\$3.85/bushel) for soft-white wheat and \$0.1643/kg (\$4.50/bushel) for hard-red wheat.

Mean yield loss for the field was calculated at 553 kg/ha (19%), equating to an economic damage estimated at \$91/ha using a market price of \$0.1643/kg.

1996—Winter wheat. Three fields planted to Stephens were surveyed during 1996. The experimental sites received 8 to 29% greater than normal amounts of rainfall, with rainfall well distributed during the autumn, winter, and spring. The only dry period occurred during March (mid-spring), when rainfall was less than half the mean annual value. *F. pseudograminearum* was the only crown rot pathogen isolated from symptomatic tissue at each location. As in 1995, also a “wet year,” most (96%) of the 3,047 tillers from six samples were in disease severity classes D₀ and D₁ (Table 5). Winter wheat tillers of increasing disease severity class were associated with significant reductions in most of the yield components measured. However, with most tillers having little or no crown rot, the overall reduction in calculated yield was negligible (<1%) and there was no significant relationship between calculated yield reduction and percentage of D₄ tillers. Grain protein content was not measured during 1996.

Inoculated field trials. Inoculation rate. Winter wheat growth and yields and crown rot incidence and severity were evaluated in the presence of increasing

rates of *F. pseudograminearum* inoculation at three locations. Seedling emergence at Echo and Moro, the two driest sites, was reduced by all rates of inoculum addition, and there was no emergence when the rate exceeded 8 g/m of row (*data not shown*). After emergence data were collected, experiments at Echo and Moro were abandoned due to sparse stands in all treatments except the control.

At Pendleton, seedling emergence was unaffected at inoculation rates up to 8 g/m of row but was strongly restricted at higher rates (*data not shown*). Native populations of the pathogens in the field caused 17% of plants (4% of tillers) to exhibit basal culm browning symptoms (severity classes D₁ to D₄) in control plots. Addition of inoculum at 1.0 g/m of row strongly increased infection percentages to 51% plants (25% tillers) but did not reduce numbers of tillers per plant. At inoculation rates of 3.3 and 8 g/m, symptoms were observed on 85 and 87% of plants (45 and 59% tillers), respectively, without affecting total numbers of tillers. Inoculation at 8 g/m resulted in 37% of tillers categorized into crown rot severity classes D₂ to D₄. Increasing disease severity class was associated ($P < 0.05$) with reduction in tiller height and kernel weight but not total weight of grain per head.

An inoculum application rate of 2.3 g/m of row was selected for subsequent studies,

based on overall consideration of seedling emergence at three locations, and of plant growth, yield components, and disease incidence and severity at Pendleton.

Cultivar nurseries. Seventeen winter wheat cultivars and one triticale cultivar were planted both with and without supplemental inoculum in six experiments at Pendleton and Moro during three crop years: 1999–2000, 2000–01, and 2001–02. Inadequate soil moisture in the seed zone caused stand failures due to irregular emergence at Moro during the first two years. Data for four experiments are presented in Table 6.

Climatic conditions influenced relative disease severity. Crown rot intensity was considered moderate at Pendleton during 1999–2000 and 2000–01. The 1999–2000 winter wheat season began during a drought but otherwise was wetter than normal. The 2000–01 season initially was wet but finished with an abnormally dry winter and spring. In contrast, crown rot intensity was very high during a season-long drought at both locations during 2001–02.

Inoculum treatments did not affect seedling emergence except at Pendleton during 2001–02, where pre-emergence damping-off reduced stands by 50% in the presence of *F. pseudograminearum* inoculum added to soil that became surface-crusts before

Table 4. Crown rot severity and yield components for 883 tillers of ‘936R’ hard-red spring wheat sampled from three sites in a single field infested by *Fusarium pseudograminearum* near Echo, OR during 1995

Plant characteristic	Disease severity class for tillers ^y					LSD _{0.05}
	D ₀	D ₁	D ₂	D ₃	D ₄	
Tillers in class (%)	48 a	7 b	12 b	16 b	17 b	22.1
Kernels/head	25.6 a	25.5 a	27.5 a	25.4 a	14.4 b	5.3
Grain protein (%)	16.0 a	16.2 ab	16.3 b	16.7 c	17.0 d	0.3
Kernel weight (mg)	33 a	29 b	30 ab	24 c	16 d	4.1
Grain weight (mg/head)	855 a	730 b	779 ab	618 c	223 d	106
Tillers with heads (%)	100 a	100 a	100 a	100 a	97 a	ns
Straw weight (g/tiller)	1.4 a	1.4 a	1.4 a	1.6 a	1.4 a	ns
Tiller height (cm)	49 a	50 a	50 a	49 a	45 a	ns
Reduction in grain yield from disease (%) ^z	0 a	1 a	3 ab	5 b	10 c	3.6

^y Crown rot severity classes were D₀ = none; D₁, D₂, and D₃ = browning up to the first, second, or third node, respectively; and D₄ = browning up to the fourth node or above. Means followed by the same letter within a row are not significantly different at $P=0.05$ according to Fisher’s least significant difference (LSD); ns = not significant.

^z Relative comparison of yields for groups of individual tillers exhibiting (D₁ to D₄) or not exhibiting (D₀) visual symptoms of crown rot.

Table 5. Crown rot severity and yield components for 3,047 tillers of ‘Stephens’ winter wheat sampled at two sites in each of three *Fusarium pseudograminearum*-infested fields in Oregon and Washington during 1996

Plant characteristic	Disease severity class for tillers ^y					LSD _{0.05}
	D ₀	D ₁	D ₂	D ₃	D ₄	
Tillers in class (%)	91 a	5 b	2 b	1 b	1 b	11.3
Kernels/head	29.3 a	28.7 a	33.1 a	24.5 a	28.1 a	Ns
Kernel weight (mg)	44 a	44 a	39 ab	39 ab	32 b	7.5
Grain weight (mg/head)	1,301 a	1,253 a	1,279 a	945 b	908 b	192
Tiller height (cm)	83 a	83 a	77 ab	77 ab	70 b	9.1
Tillers with heads (%)	95 a	92 a	93 a	90 a	91 a	ns
Straw weight (g/tiller)	2.3 a	2.4 a	2.1 ab	1.8 bc	1.7 c	0.4
Reduction in grain yield from disease (%) ^z	0 a	0 a	1 ab	5 bc	8 c	4.3

^y Crown rot severity classes were D₀ = none; D₁, D₂, and D₃ = browning up to the first, second, or third node, respectively; and D₄ = browning up to the fourth node or above. Means followed by the same letter within a row are not significantly different at $P=0.05$ according to Fisher’s least significant difference (LSD); ns = not significant.

^z Relative comparison of yields for groups of individual tillers exhibiting (D₁ to D₄) or not exhibiting (D₀) visual symptoms of crown rot.

seedling emergence. Surface crusting was caused by a single 4-mm rainfall event. Inoculum greatly increased percentages of plants with infected crown tissue in three of four experiments, with high amplitudes in year-to-year variability. Inoculation increased incidence and severity ratings for lesions on subcrown internodes for all experiments. Expression of whiteheads also was increased by inoculation for the three experiments where this parameter was measured. Grain test weight was reduced for three of four experiments. Grain yield always was reduced by inoculation. Inoculum-induced yield reduction was greatest when droughty conditions occurred throughout the crop year and was less when water was adequate for crop growth at least during one season, autumn or spring. The estimated 12% reduction in grain yield during 1999–2000 was not anticipated in that there was no commensurate amplification in expression of whiteheads in response to inoculation.

Bundle samples were collected before plots were mechanically harvested during 2000. For this article, data for the 18 entries were composited for each disease severity class, D₀ to D₄. Compared with the control, inoculation significantly reduced percentages of tillers in severity class D₀ (from 87 to 49%, LSD_{0.05} = 5) and increased percentages of tillers in classes D₁ (from 8 to 21%, LSD_{0.05} = 3), D₂ (from 4 to 19%, LSD_{0.05} = 3), and D₃ (from 0 to 9%, LSD_{0.05} = 5). Therefore, inoculation shifted the proportion of total grain yield from the D₀ class toward classes D₂ and D₃ (Fig. 2). Kernel weights for the D₃ and D₄ classes always were significantly less ($P < 0.05$) than for the D₀ and D₁ classes.

When plots were mechanically harvested, measured reductions in grain yield

in response to inoculation varied from 12 to 61% (Table 6). These reductions were in addition to those that may have occurred in response to infections by the native pathogen flora. Estimates of damage from the native flora were made only once, using the bundle samples for all control plots during 1999–2000. When tillers for each disease severity class in control plots were evaluated separately, calculations indicated that the yield loss in response to the native soil population was 8.8%. Therefore, it was estimated that the total yield loss in

inoculated plots was approximately 21% rather than the 12% reduction difference expressed between control and inoculated plots.

Eight winter malting barley cultivars and breeding lines were evaluated at Pendleton during 2003–04. Inoculation did not significantly reduce seedling stand or increase disease incidence and severity parameters (*data not presented*). Inoculation reduced grain yield from 6,716 to 5,819 kg/ha (13%; LSD_{0.05} = 573) and had no effect on test weight.

Fig. 2. Contribution of tillers in each of five crown rot severity classes (D₀ to D₄) to the total grain yield for bundle samples (1-m row length) collected from 17 winter wheat cultivars and 1 triticale cultivar during summer 2000. Half the plots for each grain entry were inoculated with *Fusarium pseudograminearum* at the time of planting during autumn 1999. Bars represent standard errors based on a variable number of heads in each disease class. Total heads from control and inoculated treatments were 16,931 and 15,926, respectively. Heads from control and inoculated treatments for each disease class were 14,780 and 7,939 for D₀, 1,923 and 3,068 for D₁, 193 and 3,089 for D₂, 32 and 1,538 for D₃, and 3 and 292 for D₄.

Table 6. Seedling establishment, crown rot incidence and severity, and yield components for 17 winter wheat cultivars and 1 triticale cultivar planted into control soil infested by a native population of *Fusarium pseudograminearum* and into soil supplemented with additional inoculum of the same pathogen^x

Sampling parameter	Pendleton						Moro	
	1999–2000		2000–01		2001–02 ^y		2001–02	
	Control	Inoc	Control	Inoc	Control	Inoc	Control	Inoc
Seedling emergence								
Plant stand density (plants/m row)	75 a	75 a	85 a	84 a	43 a	23 b	33 a	30 a
Disease intensity during early spring								
Rotted crowns (%)	13 a	54 b	tr a	1 a	1 a	29 b	1 a	4 b
Lesions on subcrown internode								
Disease incidence (%)	6 a	45 b	30 a	38 b	65 a	88 b	38 a	58 b
Disease severity (0 to 4; 4 = severe)	1.1 a	3.0 b	1.6 a	2.5 b	1.5 a	2.7 b	1.8 a	2.1 b
Mature plants								
Whiteheads (%)	tr a	1 b	1 a	4 b	...	...	8 a	29 b
Test weight (kg/m ³)	709 a	707 a	734 a	708 b	773 a	760 b	696 a	657 b
Grain yield (kg/ha)	7,552 a	6,676 b	5,799 a	5,125 b	4,316 a	1,686 b	2,158 a	1,079 b
Yield reduction from inoculation (%)	...	12 ^z	...	12	...	61	...	50

^x Means for control and inoculated treatments followed by the same letter within a row during each year are not significantly different at $P = 0.05$ according to Fisher's least significant difference. "Inoc" refers to plots in which inoculum consisting of millet seed colonized by *F. pseudograminearum* was banded at 2.3g/m of row and 2 cm above wheat seed at the time of planting; "tr" indicates a trace level of reduction (<0.05).

^y Rain caused preemergence soil crusting at Pendleton during September 2001. Crusting directly impeded emergence and also greatly amplified damage caused by the *Fusarium* spp. Stands were greatly reduced by crusting plus added *Fusarium* spp. compared with crusting alone. At Moro in September 2001, emergence was uniformly poor due to low moisture in the summer fallow.

^z Yield components from bundle samples collected from control plots were used to calculate a yield loss estimate of 8.8% from crown rot caused by a background level of naturally occurring pathogens at Pendleton during 1999–2000. Therefore, total yield reduction for inoculated plots was estimated at 21%, consisting of 9% from native pathogens and 12% from supplemental *F. pseudograminearum*.

Four spring wheat cultivars were evaluated at Moro and Pendleton during 2004. Inoculation did not significantly reduce seedling stand or increase disease incidence and severity parameters at Moro but significantly increased the incidence of rotted crowns and disease severity ratings at Pendleton (Table 7). At Pendleton, there was a significant inverse relationship ($P = 0.04$) between crown rot incidence and percentages of plants containing Hessian fly puparia under the leaf sheath. Expression of whiteheads was increased by inoculation at Moro and whiteheads were not expressed at Pendleton. Spring wheat yield was reduced 15% by inoculation at Moro but was not reduced at Pendleton. Test weights and kernel weights did not differ for spring wheat at either location.

DISCUSSION

Crown rot damage was examined on commercial fields selected arbitrarily when crown rot symptoms were not visually apparent in the aerial canopy. The average amount of damage for the 13-field survey during 1994 was 348 kg/ha or \$51/ha, representing a loss of 9.5% in potential productivity in the semiarid environment of eastern Oregon and Washington. Cultivars and climates in the surveyed fields were estimated to represent 20% of the nonirrigated winter wheat production in eastern Oregon and Washington, which was 5.1 million tonnes produced on 1.3 million ha, for a farm gate value exceeding \$700 million. Therefore, losses from crown rot in eastern Oregon and Washington during 1994 were estimated at 97 million kg or \$13 million.

The commercial field in which crown rot was most intense during 1994 occurred in Sherman County, OR. The field sustained an economic loss of \$219/ha (1,550 kg/ha). Greater losses were likely in other

commercial fields in Gilliam and Morrow Counties, OR and Klickitat County, WA, where crown rot was not examined quantitatively but appeared to be more intense than in the most severely affected fields sampled in our survey. Yields in plots inoculated with *F. pseudograminearum* were as much as 61% lower (equivalent to \$372/ha) than in adjacent plots, where the yield reduction in naturally infested (non-inoculated) plots was not quantified. The total amount of damage in inoculated plots was likely to have been of a similar magnitude to yield losses (to 89%) caused by native populations of this pathogen in Queensland, Australia (18).

Crown rot reduced grain yield by reducing kernel weight and numbers of kernels per head, as has been reported (16). Additionally, we report that crown rot reduced grain test weight, kernel weight, tiller height, and straw weight. Wheat market grades in the United States of America are established based on test weight, with reduced market prices associated with declining test weights for a specific market class (soft white, hard red, and others). Therefore, reduction in test weight has a direct effect on market value. Soft-white wheat intended for use in low-protein products would have had additional economic loss because the market grade became lower with reduced test weight and increased grain protein content. Also, straw is valued for reducing soil erosion and for maintaining soil quality. Minimum amounts of straw residue on the soil surface are required to meet compliance standards for financial incentive programs which encourage producers to utilize practices that enhance soil sustainability. Therefore, acute occurrences of crown rot are counter-productive to maintaining the soil resource and eligibility for certain federal farm programs.

This appears to be the first report that crown rot increases grain protein content and, therefore, affects market quality of soft-white winter wheat, hard-red winter wheat, and hard-red spring wheat (14). High protein content generally is considered favorable for hard wheat classes destined for use in products such as noodles and leavened breads. Low protein percentages are required for soft wheat classes destined for uses in products such as sponge cakes, cookies, crackers, and flat breads. Most wheat produced in the PNW is soft-white wheat. Therefore, occurrences of acute crown rot are likely to reduce the performance qualities for PNW wheat sold to established customers seeking low-protein soft-white wheat.

The influence of drought on crown rot incidence and severity is well documented (5,7,11,24,31). Damage is especially acute when drought occurs during seedling and post-anthesis growth stages. However, crown rot also causes some damage during wet years in semi-arid environments, in irrigated fields, and in high-rainfall regions with a summer-dominant distribution (16,20,31,36). In this study, crown rot caused most damage during years of drought (1994 and 2002) but also caused damage during two of three comparatively moist years (1995, 1996, and 2000). Our yield-loss estimates during years with precipitation above the norm for production systems in the region indicate that crown rot damage in the PNW is greater and more widespread than has been recognized previously. During 1995, we estimated that crown rot reduced wheat yield by 2%, with a range of 0 to 10% in 10 fields, equating to reduced values of \$0 to \$68/ha. Also during 1995, estimates for a single spring wheat field indicated losses from crown rot were 19% yield and \$91/ha value. In 1999–2000, yield loss from the native crown rot pathogen flora was estimated at 9%. In two years of inoculation tests near Pendleton (2000 and 2001), yield reductions 12% above those caused by the native population were observed in response to inoculation, without notable increases in occurrences of whiteheads. Therefore, it appears that low numbers of whiteheads in wheat crops in higher precipitation zones may be incorrectly interpreted to mean that crown rot is not significantly affecting yield and protein in those regions. Crown rot is more readily identified as a primary disease in drier regions because the disease becomes visually evident through an expression of whiteheads.

Economic and ecological incentives have slowly shifted wheat production practices in the PNW toward production systems that increase the magnitude of damage caused by crown rot (5,11,28,36). These systems are characterized by increased cropping frequency and higher proportions of surface residue, annual

Table 7. Seedling establishment, crown rot incidence and severity, and yield components for four cultivars of spring wheat planted at Moro and Pendleton, OR during 2004, with a comparison between plants in soil naturally infested with *Fusarium pseudograminearum* or supplemented with additional inoculum of the same pathogen²

Sampling parameter	Moro		Pendleton	
	Control	Inoc	Control	Inoc
Seedling emergence				
Plant stand density (plants/m row)	62 a	54 a	63 a	61 a
Disease intensity during early spring				
Rotted crowns (%)	16 a	13 a	1 a	11 b
Lesions on sub-crown internode				
Disease incidence (%)	34 a	29 a	31 a	51 a
Disease severity (0 to 4; 4 = severe)	1.6 a	1.5 a	1.2 a	2.1 b
Mature plants				
Plants with puparia of Hessian fly (%)	0 a	0 a	34 a	24 a
Whiteheads (%)	2 a	6 b	0 a	0 a
Kernel weight (mg)	35 a	35 a	35 a	35 a
Test weight (kg/m ³)	798 a	794 a	786 a	779 a
Grain yield (kg/ha)	3,429 a	2,903 b	2,847 a	3,002 a
Yield reduction from inoculation (%)	...	15	...	-5

² Means for control and inoculated treatments followed by the same letter within a row for each location are not significantly different at $P = 0.05$ according to Fisher's least significant difference. "Inoc" refers to plots in which inoculum consisting of millet seed colonized by *F. pseudograminearum* was banded at 2.3g/m of row and 2 cm above wheat seed at the time of planting.

spring cereals, and the hard wheat market classes. Hard wheat classes are not necessarily more susceptible to crown rot but require higher levels of fertilizer application to ensure their compliance with minimum standards for protein content and, therefore, are more subject to late-season water stress and higher severity of crown rot (11,24). Additionally, nitrogen fertilizer applied during the past six decades has acidified soils in the PNW (19,25), which has been associated with increasing incidence of crown rot (28). Alternative disease management practices such as genetic resistance must be enhanced to control crown rot losses as production practices continue to evolve in the PNW.

There is a strong interest in identifying easily quantifiable factors that predict crop damage caused by crown rot. Whitehead percentage is the most conspicuous and easily measured symptom and often is used as a subjective indicator of crown rot severity in the driest regions of the PNW, represented in this study by experiments at Moro, OR. Whitehead percentage is known to be influenced by seasonal conditions (12,17,18,20), and crown rot damage in this study occurred in the absence of appreciable whiteheads in a higher rainfall district near Pendleton, OR during 2000 and 2001. Compared with whiteheads, browning of the lower culm is considered a more reliable quantitative indicator of disease severity (12,17) but requires a labor-intensive assessment procedure. The percentage of reduction in grain yield in this region-wide study was negatively associated with percentages of tillers in the highest disease severity class (D₄) during 1994 but not 1995 or 1996. Although whiteheads and culm browning appear useful for comparing treatments within experiments, relationships between yield and quality of grain and proportions of either whiteheads or highly symptomatic basal culms were found to be too variable to predict quantitative crop damage caused by crown rot across environments in the PNW.

Several recent reports indicate that moderate levels of crown rot are tolerated without significant net loss in yield in some cropping systems and regions (3,6). During 1996, an average of 4% tillers exhibited basal culm-browning symptoms in samples collected from three fields of Stephens. No significant yield reduction was associated with those samples, presumably because the productivity of the 96% asymptomatic tillers compensated for any yield reduction in tillers affected by crown rot. Compensation is especially likely if infection occurs early during seedling growth, before such time that numbers of tillers and numbers of kernels per head were set by the plant.

Crown rot severity was enhanced and variability among replicates was reduced by adding inoculum of *F. pseudo-*

graminearum to field plots naturally infested by the same species. However, crown rot pathogens can reduce the rate of coleoptile elongation (4) and seedling emergence (12,16,20). In our study, wheat seed was treated with benomyl to reduce or eliminate seed rot or pre-emergence damping-off (12,35). Nevertheless, in several experiments, seedling emergence in inoculated plots was delayed by several days to 1 week even where stand densities ultimately were uniform between inoculated and control treatments (*unpublished data*). Delayed emergence can become important when adverse climatic conditions occur soon after planting. During 2001, emergence was reduced by 50% in inoculated soil compared with noninoculated soil in an experiment where soil became surface crusted after a very light rain. Seedling survival was greatly impeded if crusted soil also had an elevated population of *F. pseudograminearum*. Oregon and Washington have silt loam soils susceptible to crusting because of very low organic contents (<1.5%) and high levels of infestation by *F. pseudograminearum*, *F. culmorum*, or both. It is not uncommon for individual growers in those areas to find it necessary to replant as many as 1,000 ha once or even twice when as little as 3 mm of rain causes surface crusting before seedling emergence. These stand failures have been presumed to be caused by direct physical impediment to seedling emergence. Our results suggest that farm acreage impacted by replanting expenses may increase when direct physical impediment is compounded by *Fusarium* spp. seedling infections.

Winter barley and spring wheat yields were reduced 13 to 15% when inoculum of *F. pseudograminearum* was added to soil during 2004. For barley, this occurred even when measurable symptoms were no greater in inoculated than in noninoculated soil. At one location, inoculation did not lead to reduced yield of spring wheat when noninoculated plants sustained higher levels of infestation by Hessian fly (*Mayetiola destructor*). It would be of interest to determine if Hessian fly larvae are less capable of colonizing or damaging seedlings that are precolonized by *Fusarium* spp. Smiley et al. (29) previously reported that damage from crown rot and Hessian fly were additive.

Crown rot during 1994 appeared to have been caused by different pathogens at different sites, including *F. culmorum*, *F. pseudograminearum*, *Microdochium nivale*, and a combination of *B. sorokiniana* and *F. avenaceum*. These pathogens were isolated from mature plants. Kane (15) described a succession of potentially pathogenic fungi occurring in winter wheat crowns and roots over the growing season. Fedel-Moen and Harris (13) also demonstrated the potential importance of other *Fusarium* spp., such as *F. equiseti*, *F. acu-*

minatum, and *F. oxysporum*, that generally are considered less virulent or avirulent members of the root- and crown-inhabiting mycoflora associated with the crown rot syndrome. Each of these species are present in the PNW (31). Therefore, it is uncertain whether the dominant pathogens identified from mature plants in commercial fields during 1994 were the primary incitants of crown rot at that location. Nevertheless, *F. culmorum* was the primary pathogen identified at sites where crown rot damage was greatest during 1994. Cook (9,10) and Papendick and Cook (24) previously characterized *F. culmorum* as highly virulent to wheat and the dominant or only crown rot pathogen present in some areas of the PNW. In this study, during 1995, a comparatively wet year, *F. pseudograminearum* and *F. culmorum* each appeared to be dominant pathogens at sites with the highest as well as lowest amounts of damage from crown rot. The pathogens were isolated from rotted crown tissue in seedlings, providing greater assurance of primary association than is possible with rotted crowns from mature plants. This observation indicated that both species are capable of causing acute damage to wheat in the PNW.

We conclude that *Fusarium* crown rot causes greater economic damage to spring and winter wheat and winter barley than previously was documented in semiarid regions of the PNW. Damage includes seed rot, pre- and post-emergence damping-off, and reduction in straw production, grain yield, and grain quality. Production systems with even higher risk from crown rot damage are evolving in the region. Additional disease management practices are required to minimize economic losses associated with *F. pseudograminearum* and *F. culmorum*.

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